Far Eastern Entomologist

Дальневосточный энтомолог

Journal published by
Far East Branch of the
Russian Entomological Society
and Laboratory of Entomology
Institute of Biology and Pedology,
Vladivostok

Number 73: 1-16 ISSN 1026-051X June 1999

BIOLOGY AND ECOLOGY OF *STENOPSYCHE MARMORATA* NAVÁS (TRICHOPTERA: STENOPSYCHIDAE) IN THE KEDROVAYA RIVER (RUSSIAN FAR EAST)

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This paper deals with some aspects of biology and ecology of the larva of the net-spinning caddisfly *Stenopsyche marmorata*, an important component of the zoobenthos of East Palearctic mountain and foothill streams. Data on the species life history, larval retreat construction and their food composition are given. Larval growth in natural population and under experimental conditions was studied. Correlation equations between body weight and length, and between body weight and the larvae head capsule length were obtained. Parameters in the equation relating absolute growth rate to body weight were calculated. Changes of calorific values, dry and wet body weights ratio and relative ash content were observed in the course of development. Based on the correlation of production and energy expenditure correlation a coefficient of assimilated food utilization on growth (K_2) and growth-exchange coefficient (V) were obtained.

KEY WORDS: retreat construction, allometric growth, energy budget, calorific value, production, assimilation rate.

С.Л. Кочарина. Биология и экология *Stenopsyche marmorata* Navás (Trichoptera: Stenopsychidae) в реке Кедровая (Дальний Восток) // Дальне-восточный энтомолог. 1998. N 73. С. 1-16.

В статье рассматриваются некоторые аспекты биологии и экологии сетеплетущего ручейника *Stenopsyche marmorata*, личинки которого являются важным компонентом зообентоса многих горных и предгорных водотоков Восточной Палеарктики. Приведены данные по жизненному циклу вида, строению убежищ и составу пищи личинок. Изучен рост личинок ручейника в природных популяциях и в экспериментальных условиях. Получены уравнения зависимости массы тела от его длины и длины головной капсулы. Вычислены параметры в уравнении зависимости абсолютной скорости роста личинок от массы их тела. Прослежено изменение энергоемкости, отношение сухой и сырой массы и относительного содержания золы в процессе развития. На основании соотношения продукции и энергообмена получены коэффициент эффективности использования усвоенной пищи на рост (K_2) и рост-обменный коэффициент (V).

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INTRODUCTION

The caddisfly *Stenopsyche marmorata* Navás is widespread in the southern part of the Eastern Palearctic Region: from Japan,Korea, Southern Kuril Islands and Sakhalin to the Jenisei River Basin on Altaj (Russia), but in Siberia it is limited to the southern regions, where the larvae inhabit rapid foothill rivers. In the Tertiary, when it was warmer in Eurasia, their natural habits were much wider. Also fossils of this species are known from Baltic amber (Leavnidova, 1982).

Stenopsyche marmorata larvae are filter-feeding detritovores caddisflies. They are an important component of the zoobenthos in many watercourses and they form a major link in trophic ecosystems of Eastern Palearctic mountain and foothill streams. As their capture nets filter edible particles from the water, they aid in controlling transport of organic material in streams. Because of their ecological significance and widespread distribution, filter-feeding caddisflies are attracting ever more attention of specialists. Aquatic ecologists have welcomed comparative biological studies of caddisfly species from streams in different parts of the world.

The water stages of *S. marmorata* dominate in terms of biomass in the metarhithral of the Kedrovaya River, where the present study was undertaken. Results show that the mean biomass of the *S. marmorata* larvae was 77% of the biomass of the order Trichoptera or 35% of the biomass of all river zoobenthos during July 1979 - July 1980.

Some data on the biology and ecology of *S. marmorata* was already published by Kocharina (1986, 1989, 1997a,b). The present paper attempts to generalize all growth, feeding and respiration results for this species which were obtained during many years (1979-1989) in different seasons and will serve as a basis for future analysis of the functional role of detritivores in streams.

AREA OF STUDY

The Kedrovaya River is situated in the Primorsky Region of the Russian Far East and flows from the eastern slopes of the East-Manchurian Mountains to Amursky Bay (the Sea of Japan). It is a salmon river, which belongs to the "temperate-cold water" type and the foothill subtype. Description of the Kedrovaya River and its tributaries were given in detail by Levanidov (1977), Levanidova et al. (1977) and Kocharina (1989).

RESULTS AND DISCUSSION

I. *Life cycle*

Differentiation of *S. marmorata* into growth stages was based on head length, measured dorsally from the front edge of the frontoclypeus to the occipital foramen. Measurements were made under a binocular microscope MBS-I by means of an ocular-micrometer. Larvae and pupae were weighted on torsion balances WT-50, WT-250 and WT-I000. Measurements of head capsule length of *S. marmorata* in each monthly sampling fit the size with 25 mm frequency. Histograms were constructed for each month showing the obtained variations in distribution of the given character and likewise a histogram showing annual population dynamic for this species.

As for most other caddisfly species, *S. marmorata* has five larval instars (Fig. 1). The range of the coefficient of geometric progression of the head capsule length was 1.63-1.83. These data are in good agreement with similar findings of Konstantinov (1951) for chironomid larvae and Levanidova & Rubanenkova (1965) for caddisfly.

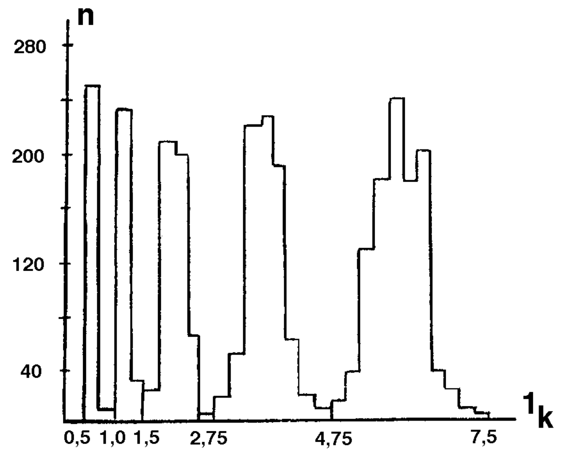


Fig. 1. Frequency distribution of the head capsule length for *S.marmorata* from the Kedrovaya River, 1979-80. Abscissa: head capsule length in mm; ordinate: number of measured specimens.

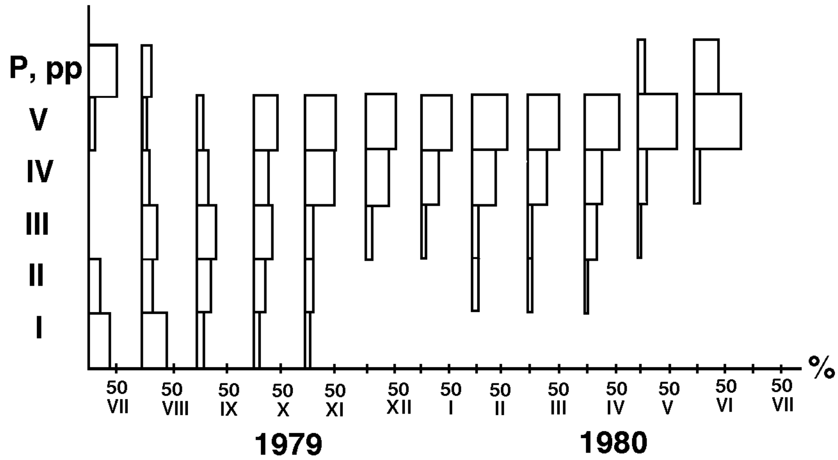


Fig. 2. Instar development in larvae of *S.marmorata* from the metarhithral of the Kedrovaya River in 1979-80 in %. I, II, III, IV, V - instars, pp - prepupae, P - pupae.

Larval abundance of *S. marmorata* relative to the density of other zoobenthos in the river was quite stable for most of the year, although in July and August as the new generation of instar I larvar appeared, the density increased sharply. In the course of development the number of instar I larvae taken in the benthometer gradually decreased, and after November they were not found in samples. Larvae overwinter as instars III-Y. During May, the number of instar Y larvae increased greatly, and all instar III larvae had passed into instar IY. The pupae began to appear in June. By the end of June the population consisted mainly of instar Y larvae and pupae. Pupae were sampled up to the last days of August (Fig. 2). Adults began to appear in late June-early July and continued to be seen for 3 months. Egg masses are round, almost black, and 2.0x1.5 cm in size. Eggs are dark-brown, ellipsoid, and range in size from 0.45x0.80 to 0.50x0.95 mm. The weight of one egg was 0.12 mg. Each egg mass contained 600-700 eggs (Kocharina, 1989).

S. marmorata in the Kedrovaya River seems to be a typical univoltine species, i.e.one-year life cycle. Only during the period of flight and oviposition (July throught Septebmer) do two generations coexist: the older (imago, pupae and larval instars III-V) and the younger (eggs and larval instars I and II).

Nishimura (1966) and Gose (1970) have also studied *S. marmorata*. Nishimura concluded, on the basis of his data that *S. marmorata* inhabiting the Maruiamagawa River (Japan, Honshu Island, Hiogo prefecture) had two generations a year, with adults emerging in May-June and in September-October. Gose data have indicated that the number of generations per year of *S. marmorata* in the rivers of Hokkaido and Honshu Islands depended on the accumulated water temperature of the water-courses during the months of larval development. He showed that in the Ena River (southern Japan), where accumulated water temperature varied from 110 to 150 °C,

population of this species had two generations per year; while in the Ikadaba River, where accumulated water temperature was from 90 to 110°C, there were 3 generations in two years; and in the Abashiri River, where accumulated water temperature during the development period varied from 55 to 90°C, this species had only one generation a year. The accumulated water temperature in the Kedrovaya River, excepting those months when larvae evidently do not develop, was 42°C. This temperature is comparable to that of the Abashiri River, which is located in the same latitude as the Kedrovaya River. Thus, the univoltine life cycle of *S. marmorata* is in agreement with that of Gose.

2. *Larval retreat construction and food*

To establish the quantitative composition of caddisfly food, the contents of larval guts were examined according to a modified method of visual estimation commonly used in the studies of feeding invertebrates (Izvekova, 1975; Kocharina, 1989). Gut contents were estimated in 20 microscopic fields for each preparation at 640x magnification. Instars III-V (25 larvae/instar) were examined in *S. marmorata*, Nets of instars III-V for *S. marmorata* were collected together with larvae. Some nets were dried and examined under scanning electron microscope at 50x magnification.

Unlike larvae of most other net-spinning caddisflies, larvae of *S. marmorata* do not build tubes. They fasten stones of different sizes by silk. All larval instars usually build retreats on the low sides of stones, and only rarely laterally. The net mesh of *S. marmorata* larvae consists of very irregular and complicated web of threads. The largest openings are about 0.4x0.7 mm.

The quantitative composition of food for larval instars III-V is shown in Table 1. Amorphous detritus was the principal food component for larval instars throughout the year, forming a considerable part of gut contents. The amount of amorphous detritus always exceeded 50% and maximal values were noted in July: for larval instar IV it was 76%, for larval instar V it was 71%. The portion of mineral detritus was small and ranged from 0.66% in May (for larval instar V) to 4.4% in December (for larval instar V).

The periphyton in larval guts was presented by diatoms (division Bacillariophyta), green algae (division Chlorophyta) and cyanobacteria («blue-green algae», division Cyanophyta). Diatoms percentages in the guts of *S. marmorata* ranged from 1.7% to 26.4% with maximum in all instars during December. About 30 species of diatoms were noted in larval guts (Kocharina, 1997b). The green algae comprised a smaller of gut contents. The maximal amount of green algae was found in May (8.1-11.5%) with the percentage of specimens green algae ranging from 0.7 to 3.3% in July, September and December. Green algae were represented by 5 species: *Bulbochaeta sp., Cosmarium sp., Ulotrix tenerrima, U. tenuissima and U. zonata.* Cyanobacteria were found in larval guts in September only and their amount was small. *Merismopedia glauca* f. *insignis*, *Oscillatoria sp*. and *Lyngbya sp*. were detected in gut contents.

Table 1

Percentage composition of food components in gut contents of *S. marmorata* larvae instar III-V

Date	Instar	Detritus		Algae			Plant vascu-lar remain	Animal material
		Mineral	Amorphous	Diatoms	Green	Blu-green		
May, 20	III	1.4	64.3	12.7	11.5	-	3.1	6.3
	IV	1.2	61.4	7.9	8.8	-	6.9	13.0
	V	0.7	64.2	12.7	8.1	-	3.3	9.9
July,6	IV	1.5	76.0	13.2	1.3	-	6.2	2.1
	V	1.1	71.3	16.3	2.6	-	4.3	4.2
September, 16	III	2.3	66.6	3.4	0.7	1.5	11.6	14.0
	IV	1.0	64.2	1.7	1.3	0.5	14.6	16.8
	V	2.2	52.3	2.4	-	3.3	22.7	17.2
December, 3	III	3.9	62.5	13.2	3.3	-	0.6	16.4
	IV	3.5	54.0	26.4	-	-	4.0	12.1
	V	4.4	55.8	17.8	2.0	-	4.9	15.0

The maximal portion of plant vascular remains was discovered in September for all larval instars; the minimal value was in December for larval instar III.

Animal material made up a small amount in May and July, and, by contrast, a considerable amount in September and December. It is possible that this phenomenon was connected with preparation for overwintering. Animals present in larval guts were representatives of the insect order Diptera: larvae of *Nymphomyia levanidovae* Rohd.et Kalug. (Nymphomyiidae) and *Orthocladius* gr. *olivaceus* K.(Chironomidae).

Thus, the quantitative analysis of gut contents showed, that all larval instars of *S. marmorata* are detritovores, thought animal remains can comprise a considerable part of food during certain periods of their life cycle.

3. *Allometric larval growth*

3.1. *Relationship of body wet weight and body length*

The correlation between length (L) of growing organism and its body wet weight (W) can be given using the following equation (Winberg,1968): $W = a L^b$, where W is body wet weight of animal in mg; L is length of body in mm; "a" and "b" are constants of equation, with "a" being a constant, equal to W, when L = 1. If the animal keeps geometrical likeness of body form in the course of growth, b=3 (indicating isometrical growth). If the ratio W/L decreases during growth, then b<3 (indicating negative allometric growth); otherwise, b>3 (indicating positive allometric growth).

In recent years this equation was used in hydrobiological investigations by Russian scientists for animal of different systematic groups. This correlation was studied for chironomid larvae (Pankratova & Balushkina, 1981; Balushkina, 1982,1987; Toderash,1984), larvae of rheophilous species of mayflies (Tiunova, 1993) and stoneflies (Teslenko, 1992) and also limnephilous species of caddisflies (Alimov & Vlasova, 1980).

This investigation determined that body wet weight is highly correlated with body length for *S. marmorata*. This strong dependence is approximated by the following equation: (Kocharina,1997a):

$$W = (0.056 \pm 0.012)\ L^{\mathbf{2.288 \pm 0.017}} \quad (1).$$

The line of regression, corresponding to this equation, is shown on Fig. 3. The relative error of the parameter "b" is small (0.74%). The correlation coefficient is about 0.96. The value of parameter "b" (2.288) in this equation shows that negative allometry is characteristic for *S. marmorata* larvae.

3.2. *Dependence of body wet weight upon length of head capsule*

Edwards (1958), Takeya (1958) and Smock (1980) showed that, for different groups of insects, the correlation of mean body wet weight and head capsule width for each instar may be described by the following equation: $W' = q\, d_k^{\,a}$, where W' is the mean body wet weight of larvae in each instar, q is the body wet weight of larvae with head capsule equal to 1 mm, d_k is the width of head capsule,

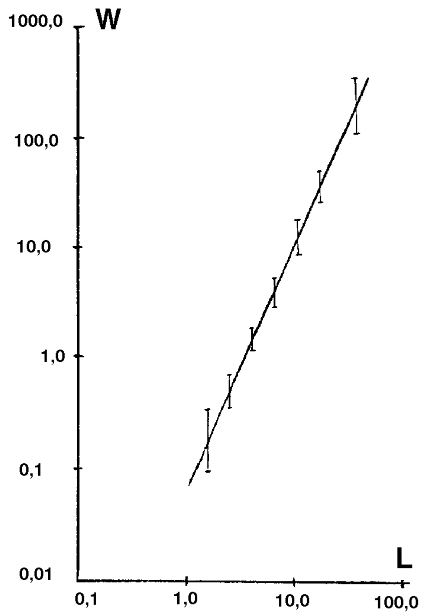


Fig. 3. Relationship between body wet weight (W in mg) and body length (L in mm) for *S.marmorata* larvae. Vertical lines indicate confidence interval at the 95% significance level.

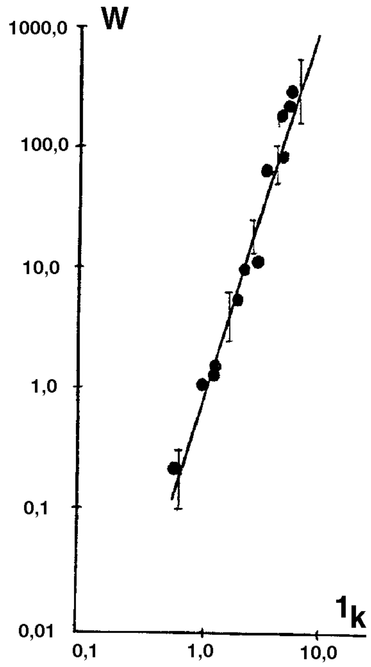


Fig. 4. Relationship between body wet weight (W in mg) and head capsule length (l_k in mm) for *S.marmorata.* Vertical lines indicate confidence intervals at the 95% significance level.

and "a" is a constant Balushkina (1987) completed analogous work for larvae of some species of Chironomidae

The dependence of the body wet weight upon length of head capsule was obtained for *S. marmorata* larvae also (Fig. 4). This dependence can be approximated using the following equation (Kocharina,1997a):

$$W = (0.791 \pm 0.098)\, l_k^{\mathbf{3.227 \pm 0.120}} \quad (2).$$

The error of the parameter "q" in this equation is 0.13%, the error of the parameter "l_k" is 4.0%. The correlation coefficient is 0.99.

4. *Dependence of absolute growth rate on body wet weight in cages and in natural population*

To study wet weight growth of *S. marmorata* two methods were used: 1) rearing larvae in cages under conditions close to natural and 2) analysis of larval age-size composition in a natural population. The first method, and also the dependence of

Table 2

Data on growth of *S. marmorata* larval in natural population of the Kedrovaya River metharhitral

Date I (t_1)	L_1, mm	Date 2 (t_2)	L_2, mm	W mean, mg	T°C mean	t_2-t_1	dW/dt (T°C=13)
13.08 79	0.99	15.09 79	5.95	0.79	13	34	0.0413
16.09 79	5.95	15.10 79	12.72	8.87	12	30	0.2436
16.10 79	12.72	14.11 79	21.90	37.13	7	30	1.1628
17.06 80	27.89	16.07 80	33.98	115.23	12	30	1.8338

growth rate on body wet weight were described by Kocharina (1989). Such dependence can be approximated by the following equation:

$$dW/dt = (0.096 \pm 0.028)\ W^{\mathbf{0.631 \pm 0.082}} \quad (3).$$

The second method we used for defining as animal growth in natural population. The histograms were constructed on the basis of quantitative samples collected in 1979-80. The curves of larval growth were determined by individual mean wet weight for each data of sampling date (Table 2). Growth rates were corrected according to Krog's curve, based on mean monthly temperature. The growth rate at 13°C (the mean water temperature in the Kedrovaya River for the period of maximal growth of the caddisflies) was set at 1.0. Growth rates measured at other temperatures were multiplied by corresponding coefficients (Winberg, 1968).

As a result of this investigation the dependence upon body wet weight was obtained, which can be presented by following equation:

$$dW/dt = 0.050\ W^{\mathbf{0.790}} \quad (4).$$

No statistically significant differences were found for larval growth of *S. marmorata* by either method (Fig.5). Therefore, one can conclude that data on larval growth obtained experimentally correctly reflects the growth of these larvae in natural populations.

5. *Calorific value, ratio of dry and wet body weights and relative ash content of larvae*

Variations of calorific value were monitored in this species from egg to imago (Kocharina, 1989). The calorific value I mg DM (dry matter) for *S. marmorata* larvae increased progressively as the animal grew from larval instar III to pupae. The calorific value of dry matter for adults is somewhat below that for pupae. Prepupal, pupal and egg stages appeared to possess the greatest calorific value in this species. This investigation determined in that dry weight is highly correlated with wet weight for *S. marmorata* during their larval development. This dependence may be described by the following equation:

$$W_w = (0.147 \pm 0.013)\ W_d^{\mathbf{1.006 \pm 0.020}} \quad (5).$$

Table 3

Relative ash content in *S.marmorata* larvae

Larval instar	II	III	IV	IV	IV	V	V	V
Dry body weight, mg	1.40	2.90	19.15	21.75	22.10	33.0	47.80	87.60
The ash content, %	14.29	12.07	9.97	7.59	7.21	6.06	5.86	4.68

The relative errors of parameters are small: for "a" - 8.84%, for "b" - 1.99%. Dry body weight averaged 15.1% in *S. marmorata*. The mean calorific value 1 mg DM of larval instars of this species was 3.77 cal/mg DM or 15.80 J/mg DM. Using equation (5), the calorific value per 1 mg wet matter (WM) for larvae of *S. marmorata.* is estimated to be 0.565 cal/mg WM or 4.77 J/mg.

To define ash content in the body of these animals, samples were heated in muffel furnace during 24 hours at 550°C (Winberg, 1968). A correlation between ash content and dry body weight was obtained for *S. marmorata* larvae. The ash content decreased in the course of growth for this species (Table 3). The mean value of ash content for *S. marmorata* was 8.47%.

6. *Energy expenditure and correlation between growth and energy expenditure in larvae*

Respiration is one of the significant functions of organisms, associated with growth rate and development of animals. One can estimate energy expenditure (R) by oxygen consumption rate (OCR or Q). Many factors influence rate and intensity of energy metabolism such as temperature, season, oxygen concentration in water, age, body size, condition of gill, and characteristics of retreats. Many investigators have concluded that body size is the main factor influencing respiration rate (RR). In recent years much data correlating RR and body wet weight have been obtained for different animal groups. The correlation between OCR (Q) of larvae and their body wet weight (W) can be presented using the following equation: $Q = Q_1 W^k$, where Q is oxygen consumption rate (OCR, ml O_2/individual.x h), W is body wet weight in g; Q_1 is the coefficient Q at W = 1. Unfortunately, there are limited data for caddisflies larvae. Some authors have obtained correlations between respiration rate and body wet weight for limnephilous species of caddisflies (Poljakova,1976; Golubkov & Vlasova, 1982; Golubkov, 1986).

This present study of the OCR (Q) of *S. marmorata* larvae was conducted in the autumn of 1984-85. Measurements of OCR were obtained from of closed bottles containing larvae in 40-160 ml respiration chambers. Chambers were established in a thermostatic aquarium. Experiments were conducted at 10°C, 11°C, 12.5°C and 16°C, with exposure time 4-5 hours.

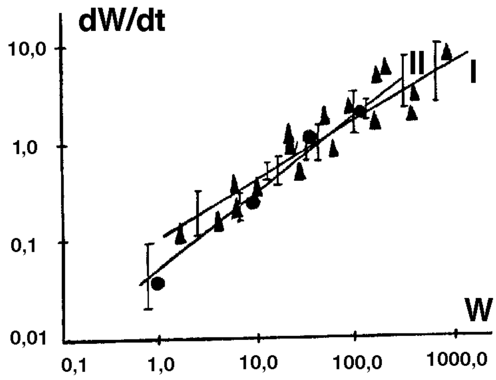


Fig. 5. Relationship between wet weight growth (dW/dt in mg/individual x h) and body wet weight (W in mg) for *S. marmorata*. I - larvae reared in cages under conditions close to natural; II - larval age class analyzed in a natural population.

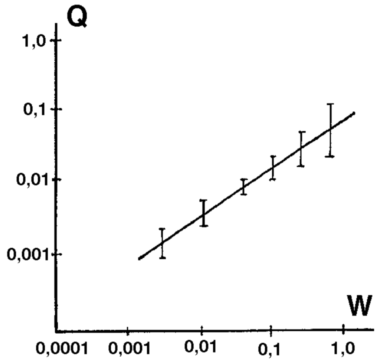


Fig. 6. Relationship between oxygen consumption rate (OCR or Q in ml O_2/individual x h) and body wet weight (W in mg) for *S. marmorata*. Vertical lines indicate confidence intervals at the 95% significance level.

To measure energy expenditure the following equation was used: R=24x4.86xQ/c, where 4.86 is the mean oxy-caloric coefficient (cal/ml O_2), Q is the oxygen consumption rate (OCR in ml O_2/individual.xh), and c is the calorific value (cal/mg).

As a result of this investigation, a relation between oxygen consumption rate and body wet weight for *S. marmorata* larvae was obtained, which may be conveniently expressed by the following equation:

$$Q = (0.055 \pm 0.004)\ W^{0.624 \pm 0.022} \quad (6).$$

The regression line is shown on Fig. 6. The relative error of Q_1 is 7.27% and k is 3.53%. The correlation coefficient is about 0.94.

The resulting OCR data permitted calculation of the correlation between energy expenditure and body wet weight for *S. marmorata* larvae, which may be approximated by the following equation:

$$R = 0.151\ W^{0.624} \text{ mg WM/individual.x24} \quad (7).$$

Production and energy expenditure of the *S. marmorata* population under study was estimated for months with a mean temperature above 4°C (July-November 1979, April-July 1980), i.e. for the time when larval wet weight growth was recorded. The larval population was divided into 49 size-classes with 1 mm intervals of larval length (Kocharina,1989). Mean wet weight, abundance, absolute growth rate, and oxygen consumption rate were estimated for each size-class. Growth rates were corrected according to Krogh's curve (see above). The results of investigations on OCR also were based on a temperature of 13°C by means of Q_{10}, which for *S. marmorata* is 2.28 (Golubkov & Kocharina, 1988).

The production (P) and energy expenditure (R) for larvae of *S. marmorata* during 1979-80 are given in Table 4. The correlation between growth rate and

Table 4

Energy budget of *S.marmorata* population in metharhitral of the Kedrovaya River for vegetation season during 1979-80

Date	N	B, kcal/m^2	W mean, mg	P, kcal/m^2	R, kcal/m^2	A, kcal/m^2	K_2
30.07-12.08 79	295	6.12	36.37	1.50	2.04	3.54	0.42
13.08-15.09 79	41	0.24	10.24	0.22	0.33	0.55	0.39
16.09-15.10 79	98	1.56	27.96	1.0	1.54	2.54	0.39
16.10-14.11 79	88	6.39	127.39	1.32	2.02	3.34	0.40
17.04-18.05 80	36	5.65	275.56	0.69	1.18	1.87	0.37
19.05-16.06 80	66	2.47	65.61	1.49	2.27	3.76	0.40
17.06-16.07 80	41	9.51	106.83	1.69	2.55	4.24	0.40
17.07-27.07 80	1120	4.45	69.73	5.58	8.05	13.63	0.41
For season:							
kcal/m^2		4.55		13.49	19.98	33.49	0.40
kJ/m^2		19.06		56.32	83.72	140.32	

energy expenditure can be expressed by means of coefficient of food assimilation to growth (K_2): K_2 = dW/dt x 1/(dW/dt + R) or K_2 =P/(P + R) = P x 1/(P + R).The relationship between growth rate and energy metabolism can be obtained also, using a growth-exchange coefficient (V): V =dW/dt : R, where dW/dt is absolute growth rate (mg WM/24) and R is energy expenditure rate (mg WM/24). V and K_2 for S. *marmorata* larvae were calculated from a ratio of the equation of correlation between growth rate (equation 3) to the equation of relationship between energy expenditure and body wet weight (equation 7):

$$V = 0.096\ W^{0.631} : 0.151\ W^{0.624} = 0.64\ W^{0.07} \quad (8).$$

Since the exponent of degree approaches 0, V = 0.64 and then K_2 is equal to 0.39. Therefore, K_2 and V remain constant during growth of larvae.

7. *Energy budget for population of S. marmorata*

The flow of energy or rate of assimilation (A) in water biocoenosis is a sum of community production (P) and energy expenditure (R) of all animals. In Russia the works on composition of energy budget were conducted for populations of mollusks (Alimov, 1981), chironomid larvae (Balushkina, 1987), rheophilous species of mayfly (Tiunova, 1993) and stonefly (Teslenko,1992). These investigators showed that P is function of R and it is similar in populations of different animals.

The energy budget in a population of *S. marmorata* was calculated from data about their number, age composition, biomass, production and energy expenditure

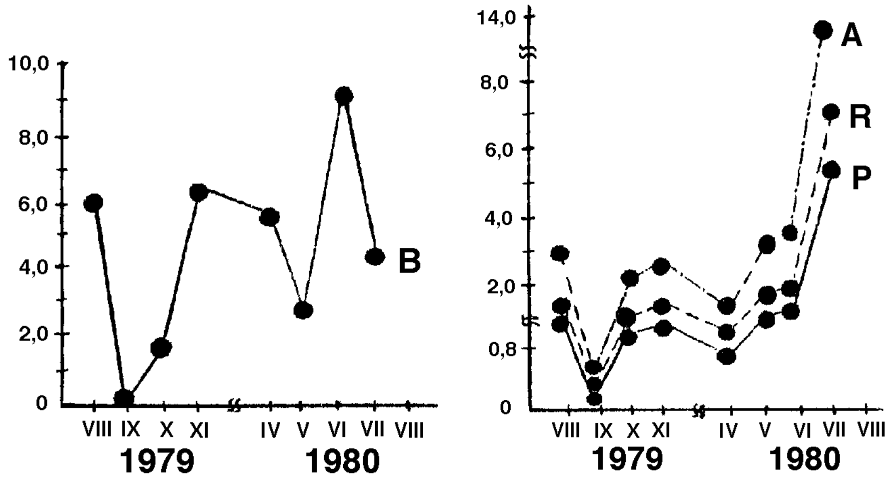


Fig. 7. Seasonal dynamics of biomass (B in kcal/m^2), assimilation (A in kcal/m^2), production (P in kcal/m^2) and energy expenditure (R in kcal/m^2) for *S. marmorata* from the Kedrovaya River.

in the course of individual development. Table 4 give values of an energy budget for population of *S. marmorata*.

The rate of assimilation in a population of animal has similar character of season changes with biomass and is in direct dependence: $A_p = a\ B^{\ c}$ kcal/m^2, where A_p is the rate of assimilation in kcal/m^2, B is biomass in kcal/m^2, and "a" and "c" are the coefficients of the equation. The assimilation rate for the population of *S. marmorata* changes with biomass seasonally (Fig. 7) and can approximated by the equation:

$$A_p = (1.265 \pm 0.015)\ B^{\ \mathbf{0.573 \pm 0.076}}\ \text{kcal/m}^2 \quad (9)$$

for vegetation season (Fig. 8). The error of the parameter "a" in equation (9) is 1.2% and of parameter "c" is 13.3%. The correlation coefficient is about 0.87.

For the *S. marmorata* population, it was established that the dependence of energy expenditure upon production by season may be described by the equation:

$$R = 0.843\ P^{\ \mathbf{1.13}}\ \text{kcal/m}^2 \quad (10).$$

If index of degree in equation (10) is 1.0, then

$P = R/0.843$ kcal/m^2 or $P/R = 1 : 0.843 = 1.19$, and $K_2 = 1.19 : 2.29 = 0.54$ (11).

The efficiency of production, or K_2 of the population, must be higher when the population consist of younger individuals, generally, which have high values of K_2. In *S. marmorata* larvae, for example, K_2 was larger during the period from 30 July to 12 August (0.42), when early instars dominated in the population. On the contrary, when the population consisted of larval instars IV and V (17 April to 18

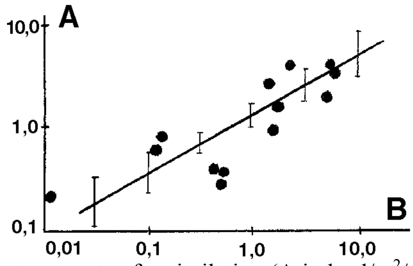


Fig.8. Relationship between rate of assimilation (A in kcal/m^2/month) and biomass (B in kcal/m^2/month) for *S. marmorata* in the Kedrovaya River.

May), K_2 had a minimal value (0.37). From 19 May to 27 July, when larvae of early instars began to re-appear in the population, K_2 increased again (0.40-41).

Therefore, the analysis of the present data showed that the efficiency of larval growth in *S. marmorata* remains at a high level during the course of development, i.e. larvae of this species transfer the organic matter on next trophic level with high efficiency.

CONCLUSION

Unfortunately there are no experimental data on food consumption rate by larvae of *S. marmorata*. Therefore, it was not possible to calculate the full energy budget for the study population of this species. However, in many respects, the functional ecology of *S. marmorata*, is typical of that for other aquatic insects. All equations were calculated for a wide range of larval weights and can reflect satisfactorily the obtained dependences.

Therefore, the present investigation can serve as a reasonable model with respect to quantitative value of this species' participation in processes occurring in freshwater ecosystems. Undoubtedly, the role of *S. marmorata* larvae in these ecosystems is very important. On the one hand, the larvae, procesing CPOM, give FPOM to collecting and filtering freshwater invertebrates. On the other hand, the larvae of *S. marmorata* are detritovore and serve by food for predators, i.e. they transfer energy to higher trophic levels.

ACKNOWLEDGEMENTS

I should like to thank my colleagues T. M. Tiunova, V. A. Teslenko and T. I. Arefina of the Production Hydrobiology Group, Hydrobiology Laboratory, for help in collecting and processing speciments. Also I express thanks to Dr. John Morse and Dr.John McCreadie for their critical remarks and for correcting the English of my manuscript.

The work was supported by the Russian Fund of Fundamental Investigations (grant N 96-04-51019).

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